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Generation length for mammals

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Abstract

Generation length (GL) is defined as the average age of parents of the current cohort, reflecting the turnover rate of breeding individuals in a population. GL is a fundamental piece of information for population ecology as well as for measuring species threat status (e.g. in the IUCN Red List). Here we present a dataset including GL records for all extant mammal species (n=5427). We first reviewed all data on GL published in the IUCN Red List database. We then calculated a value for species with available reproductive parameters (reproductive life span and age at first reproduction). We assigned to missing-data species a mean GL value from congeneric or confamilial species (depending on data availability). Finally, for a few remaining species, we assigned mean GL values from species with similar body mass and belonging to the same order. Our work provides the first attempt to complete a database of GL for mammals; it will be an essential reference point for all conservation-related studies that need pragmatic information on species GL, such as population dynamics and applications of the IUCN Red List assessment.

Keywords

Age at first reproduction, conservation assessment, IUCN Red List, longevity, reproductive life span

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Introduction

Generation length (GL) has been defined in a number of ways and has been approximated with a number of different formulas (IUCN 2013). The two most common definitions of GL are: 1) "the average age of parents of the current cohort" (IUCN 2001, 2012b), 2) "the age at which half of total reproductive output is achieved by an individual" (IUCN 2004). GL is a key vital statistic of animal populations and is used in a multitude of ecological analyses (Gaillard et al. 2005, Perry et al. 2005, Jiguet et al. 2007). In IUCN Red List assessments, GL is used as a reference time-frame to assess a species extinction risk due to population reduction (criterion A), continuing decline of small populations over a definite time period (criterion C1; IUCN 2012b), calculated extinction probability (criterion E; Mace et al. 2008). Nonetheless, such an important variable is often hard to calculate due to the paucity of detailed reproductive data. Therefore it is missing for most species, even among relatively well-studied groups such as mammals. Methods to fill missing-data gaps in biological datasets, such as multiple imputation, have been applied in mammals (e.g. Di Marco et al. 2012). However, such methods depend largely on data availability and assume that missing data are distributed randomly (e.g. among orders). We address this gap and provide the first attempt to complete a database of GL for mammals based on recently published datasets, using published metrics as well as taxonomic and allometric species relationships.

Taxonomic coverage

This database covers all 5427 extant species in the class Mammalia. The taxonomy follows the IUCN Red List of Threatened Species version 2012.2.

Methods

For 439 species, we used stated GL in years available from published IUCN Red List assessments (IUCN 2012a); for 822 additional species we derived GLs from data on species' reproductive life span and age at first reproduction (see Generation Length model, below). We obtained life-history traits from PanTHERIA (Jones et al. 2009) and AnAge (Tacutu et al. 2013). Moreover, for carnivores and ungulates, we applied a multiple imputation procedure to estimate missing values of life history variables (see below for a detailed description). We compiled the GL values of 3722 remaining species by assigning them the mean GL value of congeneric or confamilial species (when expert-based GL values of congeneric species were not available) in the same bin of log body mass.

For the mammal body masses, we used PanTHERIA (Jones et al. 2009) as our main reference, and complemented the missing data with numerous other sources, including books and primary literature (see Appendix). For species that lacked body mass data (1047), we calculated the average body mass of congeneric or confamilial species.

For 315 species, lacking a congeneric or confamilial species in the same bin of log body mass, we assigned the mean GL value of congenerics or confamilials, irrespective of their body mass. For the remaining species (n=116, 2.1 % of the total), where no information was available for congeneric or confamilial species, we assigned the mean GL value of species in the same bin of log body mass, belonging to the same order, or simply the mean GL values of the order (2 species, *Ptilocercus lowii* and *Cyclopes didactylus*). We made an exception for the two species of Dermoptera and 9 species of small mammals (body mass < 100 g); since they were the only representatives of their orders, we estimated mean GLs from species belonging to the same bin of log body mass. In this way, we obtained a GL value for all existing 5427 mammals.

Generation length model

We estimated GL for mammals from information on species age at first reproduction and reproductive life span, by applying the methodology described in the IUCN Red List Guidelines (IUCN 2013):

$$GL = R_{span} * z + AFR \quad \text{(eq. 1)}$$

where *Rspan* is the species reproductive life span, calculated as the difference between the age at last reproduction and the age at first reproduction (AFR), and z is a constant "depending on survivorship and relative fecundity of young vs. old individuals in the population" (IUCN 2013). Generation length values in the Red List are typically provided for threatened species (Vulnerable to Critically Endangered) assessed under criteria A and C1 (IUCN 2001). As largely discussed (e.g. Purvis et al. 2000; Cardillo et al. 2005), threatened species are generally characterised by relatively slow life histories respect to non-threatened species (e.g. they are generally larger, have longer gestation times, smaller litter sizes etc.). This has a potential to bias the fitting of GL model parameter toward long-living species respect to short-living ones. Nonetheless, a moderate change in the z parameter, e.g. z=0.29 in our model (calculated as the slope of the linear regression between GL and Rspan for 221 species) vs the theoretical threshold of 0.5 proposed in IUCN guidelines, will have little influence on the calculation of a GL value for short-living species (such as most of rodents), e.g. their modelled GL will remain below 3.3 years in any case (i.e. the arbitrary threshold adopted for short-generation species in the Red List). For those 221 species with GL data reported in IUCN Red List assessments, we modelled the linear relationship between expert-based GL values and calculated GL values (from reproductive life span and age at first reproduction). We found a good fit (R^2=0.84) and a high correlation (cor=0.92, p-value of the Pearson's test < 2.2e-16), which indicate a good correspondence between reported and calculated GL values, and we are confident that this is a good validation of the overall validity of the GL data reported in the IUCN Red List for mammals. Discrepancies between the calculated GLs and the GLs IUCN might

be a mix of process uncertainty (errors in the model) and observation uncertainty (errors in expert-based GL estimates), which are impossible to tease apart.

Since age at last reproduction is generally related to longevity in the wild (IUCN 2013), we assumed it to be equal to the maximum known longevity of the species. Even if published data on maximum longevity often refer to captive individuals, which might cause biases in Rspan estimates, we believe that these biases will probably influence only a limited number of large-bodied species. Moreover, since data on GL stated from experts were available for the majority of large-body species, we reduced the risk of using inaccurate data. We assumed AFR to be equal to age at first birth following IUCN guidelines (IUCN 2013). When information on age at first reproduction for a species was not available, we estimated it by summing gestation length and age at female sexual maturity. For species without empirical data on age at first reproduction for females, we used age at sexual maturity for males.

For carnivore and ungulate species, we completed missing data on maximum longevity and age at sexual maturity through a multiple imputation procedure (Rubin 1987). Carnivores and ungulates are generally characterized by lower levels of missing life-history data respect to other mammal groups (e.g. see Jones et al. 2009). Reproductive parameters used in our analyses were available for over 50% of species among Carnivora, Cetartiodactyla and Perissodactyla. Missing life-history traits were imputed, separately for carnivores and ungulates, following the procedure described in Di Marco et al. (2012). In both datasets, all missing data were imputed 10 times in order to obtain 10 complete datasets for each group. Finally, a median value was calculated for all imputed data for maximum longevity and sexual maturity for each species. Multiple imputation analyses were conducted in R using the package MICE (van Buuren and Groothuis-Oudshoorn 2010).

Dataset description

The dataset includes generation lengths for 5427 mammal species. Fields given are:

1. TaxID: identification number of species;
2. Order;
3. Family;
4. Genus;
5. ScientificName;
6. AdultBodyMass_g: body mass of species in grams;
7. Sources_AdultBodyMass: AnAge, Animal Diversity, Encyclopedia of Life (eol.org/), Nowak and Paradiso 1999, PanTHERIA, Smith et al. 2003, Verde Arregoitia et al. 2013, Mean congenerics, Mean_confamilials;
8. Max_longevity_d: maximum longevity (days) mediated from PanTHERIA, AnAge and Carn_Ung (multiple imputation for carnivores and ungulates);

9. Sources_Max_longevity: AnAge, Carn_ung (multiple imputation for ungulates and carnivores) and PanTHERIA;
10. CalculatedRspan_d: reproductive life span (days) calculated from maximum longevity and age at first reproduction;
11. AFR_d; age at first reproduction (days);
12. Data_AFR: calculated or published data;
13. CalculatedGL_d: GL (days) calculated from reproductive life span and age at first reproduction;
14. GenerationLength_d: best known estimate of GL (days), including information taken from IUCN database, calculated data and mean estimates;
15. Sources_GL:

- GMA (IUCN Red List data);
- Rspan-AFB (GL calculated as the difference between reproductive life span and age at first birth);
- Rspan-AFR(SM+Gest) (when data on age at first reproduction were not available, we calculated this parameter as the sum between age at female sexual maturity and gestation length);
- Rspan-ASMmales (GL calculated with age at sexual maturity for males, when data on age at first reproduction for females were not available);
- Mean_congenerics_same_body_mass (mean GL calculated from congeneric species in the same bin of log body mass);
- Mean_congenerics (mean GL calculated from congeneric species, irrespective of body mass);
- Mean_family_same_body_mass (mean GL calculated from confamilial species in the same bin of log body mass);
- Mean_family (mean GL calculated from confamilial species, irrespective of body mass);
- Mean_order_same_mass (for species with unknown parameter estimates, we assigned the mean GL value of species in the same bin of log body mass and belonging to the same order);
- Mean_order (mean GL calculated from species belonging to the same order, irrespective of body mass);
- Mean_all_orders_same_body_mass (species for which we estimated mean GL from species belonging to the same bin of log body mass).

Data sources

The data underpinning the analysis reported in this paper are deposited in the Dryad Data Repository at http://doi.org/10.5061/dryad.gd0m3

Original source

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References

Boyles JG, Cryan PM, McCracken GF, Kunz TH (2011) Economic importance of bats in agriculture. Science 332(6025): 41–42. doi: 10.1126/science.1201366

Cardillo M, Mace GM, Jones KE, Bielby J, Bininda-Emonds ORP, Sechrest W, Purvis A (2005) Multiple causes of high extinction risk in large mammal species. Science 309(5738): 1239–1241. doi: 10.1126/science.1116030

Di Marco M, Possingham HP, Wilson KA, Blomberg SP, Boitani L, Rondinini C (2012) ANovel Approach for Global Mammal Extinction Risk Reduction. Conservation Letters 28–66.

Fa J, Currie D, Meeuwig J (2003) Bushmeat and food security in the Congo Basin: linkages between wild- life and people's future. Environ. Conserv. 30: 71–78. doi: 10.1017/S0376892903000067

Gaillard JM, Yoccoz NG, Lebreton J-D, Bonenfant C, Devillard S, Loison A, Pontier D, and Allaine D (2005) Generation Time: A Reliable Metric to Measure Life-History Variation among Mammalian Populations. The American Naturalist, Vol. 166, No. 1, 119–123. doi: 10.1086/430330

Hoyt E (2000) Whale watching 2000: worldwide tourism numbers, expenditures, and expanding socioeconomic benefits. International Fund for Animal Welfare, Crowborough, UK.

IUCN (2001) IUCNRed List Categories and Criteria: Version 3.1. IUCNSpecies Survival Commission. IUCN, Gland, Switzerland and Cambridge, U.K.

IUCN (2004) Guidelines for Using the IUCNRed List Categories and Criteria. Standards and Petitions Subcommittee. http://www.globaltrees.org/downloads/RedListGuidelines.pdf [accessed 2013-3-10]

IUCN (2012a) The IUCNRed List of Threatened Species. Version 2012.2. http://www.iucnredlist.org [accessed 2013-3-18]

IUCN (2012b) IUCNRed List Categories and Criteria: Version 3.1. Second edition. IUCN, Gland, Switzerland and Cambridge, UK. http://www.iucnredlist.org/technical-documents/categories-and-criteria [accessed 2013-3-18]

IUCN (2013) Guidelines for Using the IUCNRed List Categories and Criteria. Version 10. Standards and Petitions Subcommittee. http://www.iucnredlist.org/documents/RedListGuidelines.pdf [accessed 2013-3-10]

Jiguet F, Gadot A-S, Julliard R, Newson SE, Couvet D (2007) Climate envelope, life history traits and the resilience of birds facing global change. Global Change Biology 13: 1672–1684. doi: 10.1111/j.1365-2486.2007.01386.x

Jones K, Bielby J, Cardillo M, Fritz S, O'Dell J, Orme CDL, Safi K, Sechrest W, Boakes EH, Carbone C, Connolly C, Cutts MJ, Foster JK, Grenyer R, Habib M, Plaster CA, Price SA,

Rigby EA, Rist J, Teacher A, Bininda-Emonds ORP, Gittleman JL, Mace GM, Purvis A, Michener WK (2009) PanTHERIA: a species-level database of life history, ecology, and geography of extant and recently extinct mammals. Ecology 90(9): 2648. doi: 10.1890/08-1494.1

Kunz TH, Braun de Torrez E, Bauer D, Lobova T, Fleming TH (2011) Ecosystem services provided by bats. Annals of the New York Academy of Sciences 1223: 1–38. doi: 10.1111/j.1749-6632.2011.06004.x

Mace GM, Collar NJ, Gaston KJ, Hilton-Taylor C, Akçakaya HR, Leader-Williams N, Millner-Gulland AJ, Stuart SN (2008) Quantification of extinction risk: IUCN's system for classifying threatened species. Conservation Biology 22: 1424–1442. doi: 10.1111/j.1523-1739.2008.01044.x

Nowak RM, Paradiso JL (1999) Walker's mammals of the world. Vol. 1. Baltimore and London, UK.

Perry AL, Low PJ, Ellis JR, Reynolds JD (2005) Climate change and distribution shifts in marine fishes. Science 308: 1912–1915. doi: 10.1126/science.1111322

Purvis A, Gittleman JL, Cowlishaw G, Mace GM (2000) Predicting extinction risk in declining species. Proceedings of the Royal Society B 267(1456): 1947–1952. doi: 10.1098/rspb.2000.1234

Rubin DB (1987) Multiple imputation for nonresponse in surveys. Wiley Online Library.

Smith FA, Lyons SK, Ernest SKM, Jones KE, Kaufman DM, Dayan T, Marquet PA, Brown JH, Haskell JP (2003) Body mass of late quaternary mammals. Ecology 84: 87131.

Tacutu R, Craig T, Budovsky A (2013) Human Ageing Genomic Resources: Integrated databases and tools for the biology and genetics of ageing. Nucleic Acids Research 41: 1027–1033. doi: 10.1093/nar/gks1155

van Buuren S, Groothuis-Oudshoorn K (2010) MICE: Multivariate Imputation by Chained. JStat Softw VV: 1–68.

Verde Arregoitia LD, Blomberg SP, Fisher DO (2013) Phylogenetic correlates of extinction risk in mammals: species in older lineages are not at greater risk. Proceedings. Biological sciences / The Royal Society 280: 20131092. doi: 10.1098/rspb.2013.1092

Appendix

Database on generation length of mammals. (doi: 10.3897/natureconservation.5.5734.app). File format: Microsoft Excel file (xls).

Explanation note: Database on generation length of all extant mammals, with 5427 records.

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